Mammalian Sociality

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Abstract Mammals generally form social groups to gain better protection from or to capture prey more efficiently. Open habitats are especially conducive to group formation because in those habitats social defenses are most effective at deterring predators .Closed habitats are more conducive to solitary living because then concealment is ofen the best defense against predation. Group size is typically limited by competition for resources, and hense it is usually larger when food is clumped or relatively abundant. Social organization often revolves around status relationship, which are frequently based on agonistic interactions.

Key words: Sociality, Behaviour, Optimal model

Costs and Benefits of Group living

Several costs of group living impede the evolution of sociality in mammals. Competition for resources and mates is intensified whenever individuals join together as social groups.

Social Ungulates

Social ungulates clearly gain protection from predators by living in social groups. Nearly all ungulates are vulnerable to predators, at least when young, and sociality provides several modes of defense not available to solitary individuals. Member of social groups are probably better able to detect stalking predators by depending on mutual vigilance, and characteristic alter postures or alarm signals provide the means for making mutual vigilance work. Sudden flight, stiff-legged bounding gaits, and conspicuous rump patches or hind leg markings all communicate danger exploding erratically in directions. Individuals may thwart attacks by bunching tightly together, exploding erratically in all directions, zigzagging through a herd, or even counterattacking. These defenses are all effective,depending on type of predator, group size and environmental circumstances, but not all ungulates employ them to the same degree. Some species live as solitary individuals, replying on concealment or other defenses for protection, while others live in groups of various sizes. A particularly interesting problem is to understand why some species rely on social defenses while others do not.

Individuals can adopt social defense tactics only if the cost of sociality are not too high.

Jarman's(1974) analysis reveals the general relationships between foraging ecology, habitat structure, group size and body size.It makes clear that sociality in ungulates is related to habitat structure as well as food distribution and abundance. Thus the combined influences of food availability and antipredator tactics make social grouping behavior most prevalent in open habitats and prevalent in closed habitats.

Gao Zhongxin (1996) evaluated benefits of sociality for mongolia gazelle by relating their foraging ecology to group size. Social Mongolian gazelle clearly gain protection from wolf by living in social group on open glassland.

Social Primates

In comparison with ungulates, the observed frequency of predation on primates is small. This has sometimes been construed as evidence that predation is not an important selective factor favoring sociality. However, predation on primates may be more difficult to observe or it may be rare because sociality is an effective defence against predation.

The number of predators capable of attacking primates are numberous. That sociality is an important defense against predators is indicated by several lines of evidence. Social primates generally rely on mutual vigilance to detect predators, with many species employing specialized alarm calls to signal danger. Early detection of predators is an important advantage, as it provides group members with more time to escape up trees or onto cliffs. Male baboons and patas monkeys often act as sentinels while other troop members forage or conduct other activities. Male patas monkeys and guenons often distract predators by leaping against small bushes and then leading them away from the female group. Thus primate sociality does appear im-

portant as means of predator defence.

Social defenses against predation generally become more effective as group size increases. and yet primate groups vary greatly in size. both within and among species. This implies that the net benefits derived from sociality vary from one group to another. probably because vulnerblity to predation or cost of competition vary between groups. Most theorists have attributed variations in group size to the latter.

The some patterns show that predation pressure and the distribution and abundance of safe sleeping sites and food resources affect the overall social structure of primates.

Social Carnivores

Social carnivores can potentially benefit from cooperation in at least four ways.

All social carnivores studied to date hunt more effectively in groups than when alone, an advantage that in generally accepted as the most important reason favoring their sociality, cooperation improves hunting success in two ways. It enables capture of large prey animals, and it increases the percentage of hunts that result in kills. The importance of each advantage varies, depending on the predator and prey species involved.

Benefits gained from cooperatively protecting carcasses

In Africa cooperation improves the ability of carnivores to protect carcasses from scavengers or to steal carcasses from other predators, lions and hyenas regularly compete for carcasses and obtain significant amounts of food through thievery. A single lion usually can not prevent a pack of hyenas or wild dogs from stealing a carcass, but two or more lions can. Similarly, groups of lions can successfully steal food from hyena packs, while single lion can not (Figure 1).

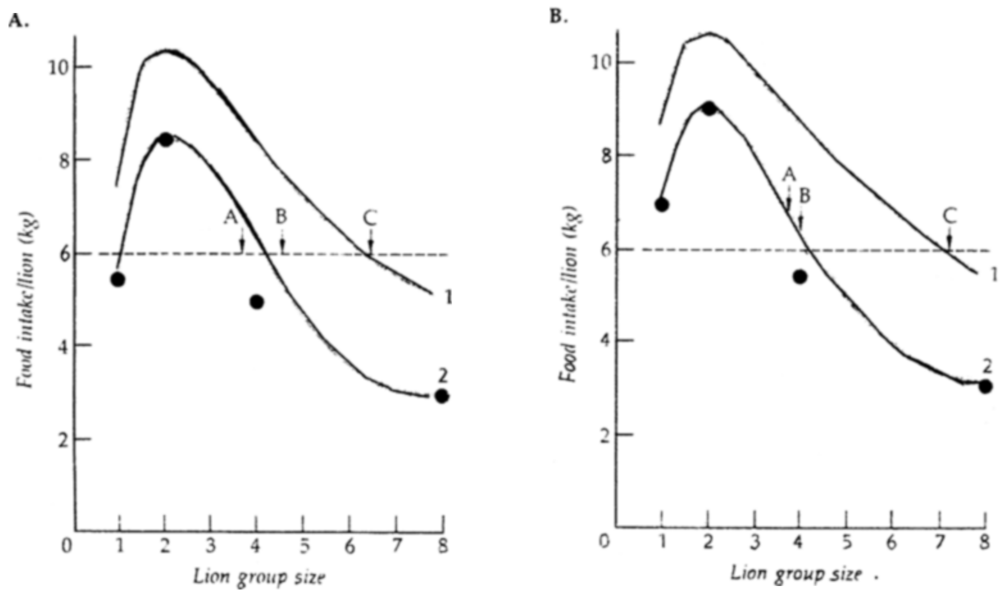

Fig. 1 The effect of lion hunting-group size on food intake rate per lion.

Mean edible prey biomass (kg) captured per chase each day is plotted against the size of hunting groups Curve 1 gives hypothesized intake rates during the wet season Curve 2 gives hypothesized intake rates during the dry eeason Dashed lion indicate minimum daily food requirements per lion. Observed mean lion group sizes are given for the eastern plains of Serengeti National Park (dry season) (A), the western woodlands (dry season) (B) , and the border region (wet season) (C). A Data for attacks on wildebeest B Data for attacks on zebra

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Benefits gained from reduced risk of injury while hunting.

Cooperation may reduce the risk of being injured or killed during a hunt , but the importance of this possible benefit is difficult to assess. Predators certainly risk injury when hunting large or dangerous prey.

Benefit gained from cooperative defense against predators

A common benefit of sociality in vertebrates is better protection from predators. Grouping behavior and cooperation are beneficial to social carvivores because they enable more efficient and safer hunting, better

protection of carcasses, and enhanced capability of stealing carcasses. The relative importance of each benefit varies with species.

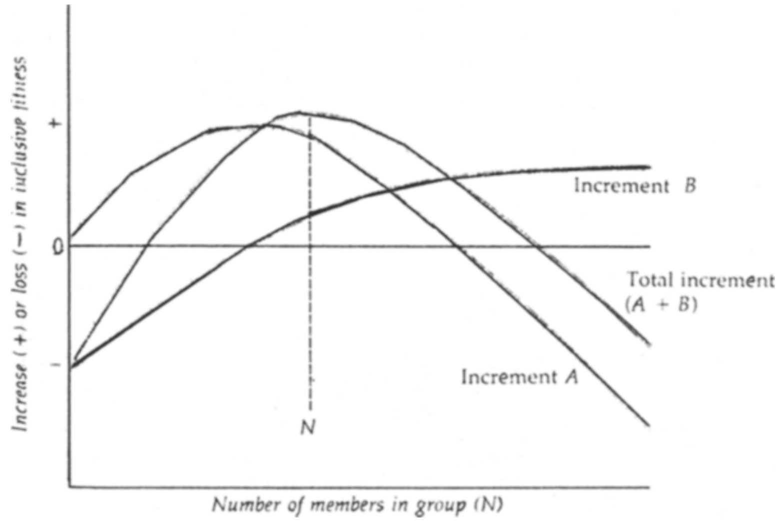

Fig. 2 A model of optimum group size

The vertical axis indicates the gain or loss of inclusive fitness arising as a result of a given group size. The horizontal axis gives group size. The curves labeled Increment A and Increment B (broken lines) indicate the fitness effects of two different selective factors (e.g., predator defense and cooperative hunting) that affect group size. The sum of increments A and B (solid line) represents the total effect of all selective fators affecting group size. Optimum group size (N) occurs where the positive effect of inclusive fitness of all selective factors combined is maximal.

Source: from E. O. Wilson, Sociobiology: The New Synthesis (Cembrige, Mass.: Belknap Press of Harvard University Press, 1975), p. 136. Reprinted by permission

Determinant of Group Size

Above sections have discussed in a qualitative way, the benefits and costs associated with sociality. The qualitative aspect of this same issue is group size. The magnitude of both costs and benefits should vary as a function of group size, and if it does, the net benefit derived from sociality will be maximal at some optimum size. The optimum size is very likely to differ for each individual in a group,since both costs and benefits should vary according to the individual's sex,age and social status.

Models of Optimal Group Size

One way predicting optimal group size is to plot the separate effects of each selective factor affecting a particular individual's inclusive fitness as a function of group size (Fig. 2), optimal group size for any particular individual is given by the point where the combined effects of all selective factors maximize that individual's inclusive fitness.

Wilson's (1975 a) model is a useful way to visualize the complexities of the group size problem, but it is difficult to employ in practice.

A second approch for predicting optimal group size is to compute lifetime reproductive output of group member as a function of group size. The model developed from this approach calculates optimal group size for average female in a social group, but a better procedure would be to calculate separate optima for each individual or status level in the group.

The model predicts that sociality among vetebrates can evolve in four basic ways (Fig. 3). In case 1, adult female survival rate increases with increaseing group size while adult female reproductive rate decreases. In case 2, female survival rate decreases with increasing group size while reproductive rate increases. In case 3, female survival rate and reproductive rate both increase initially with increasing group size, but group size is limited by an eventual decline in reproductive rate. Case 4 is indentical to case 3 except that group size is limited by a decline in survival rate instead of reproductive rate.

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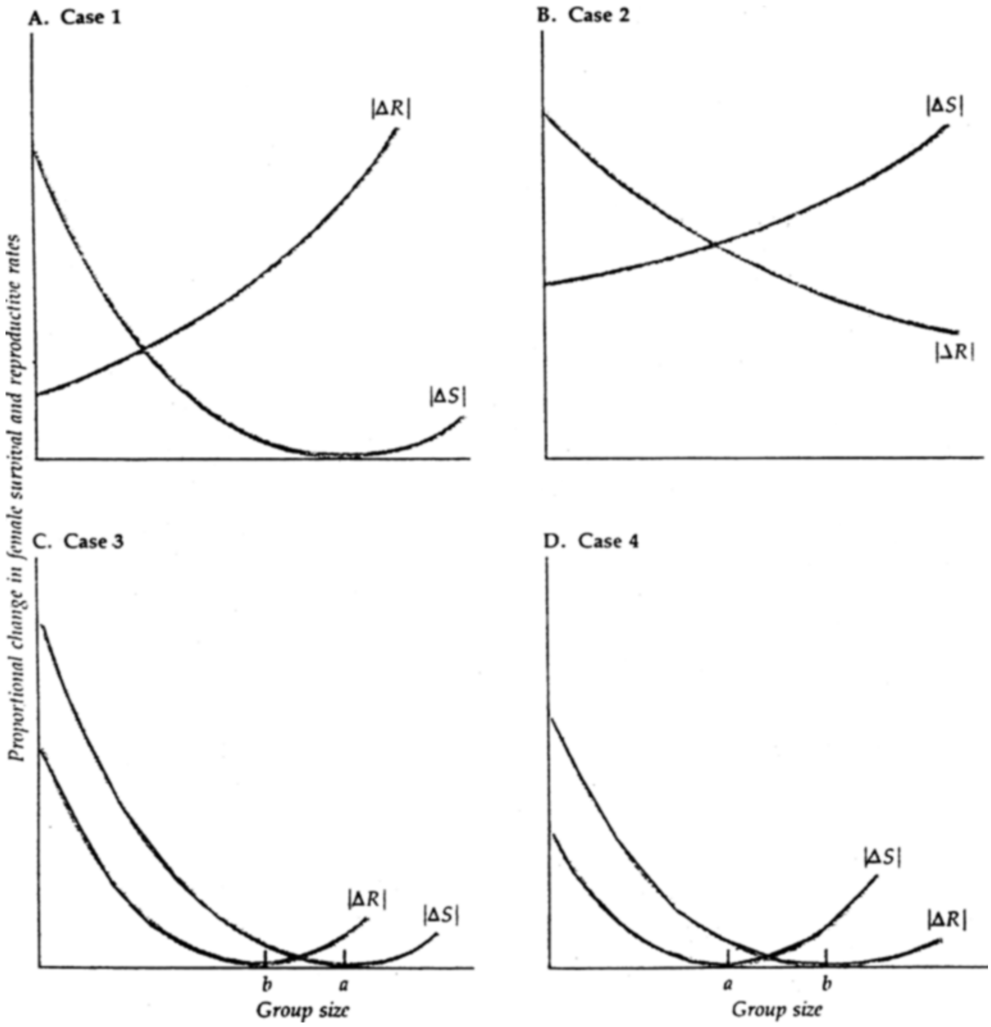

Fig. 3 The four cases of Wittenberger's model of optimum group size

The curve labeled $|\Delta R|$ represents the proportional change (either + or -) in female reproductive rate arising when a group cintaining a given number of females gains one additional adult female mumber. The curve labeled $|\Delta S|$ respresents the proportional change (either + or -) in female survival rate arising when a group containing a given number of adult females gains one additional adult female member. The magnitude of change ($|\Delta R|$ and $|\Delta S|$ varies with group size. Optimal group size occurs at the point where the $|\Delta R|$ and $|\Delta S|$ curves intersect. A. In Case 1 of the model. female reproduvtive rate decreases with increasing group size ($|\Delta R|$ <0). while female survival rate increases ($|\Delta S|$ >0). B. In Case 2 of the model. female reproductive rate increases with increasing group size ($|\Delta R|$ >0). while female survival rate decreases ($|\Delta S|$ <0). C. and D. In Case 3 and 4 of the model. female reproductive rate increases until group size = ($|\Delta R|$ >0) and then decreases ($\Delta R<0$). Female survival increases until group size= a($\Delta S>0$) and then decreases ($\Delta S<0$). Case 3 occurs when reproductive rate begins decreasing before survival rate. Case 4 occurs when survival rate begins decreasing before reproductive rate.